34. Soil Effects Mediate Interaction of Dogwood Anthracnose and Acidic Precipitation

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Dogwood anthracnose is a fungal disease caused by *Discula destructiva* Redlin. It was first reported in 1976 (Byther et al., 1979), and spread rapidly throughout the range of the Pacific dogwood (*Cornus nuttallii* Audubon) on the west coast. The disease was found in 1978 in New York, and swept through the eastern flowering dogwood (*Cornus florida* L.) population as far south as northern Alabama in just fifteen years (Redlin, 1991). This rapid spread led to speculation that the fungus may be exotic (Redlin, 1991), but *D. destructiva* has not been found elsewhere. Another theory is that such environmental factors as hard winters or air pollution, may have increased dogwood susceptibility (Hibben and Daughtrey, 1988; Hudler, 1985).

The relationship between acidic deposition and forest tree diseases has been the subject of much debate (Grzywacz and Wazny, 1973; Johnson and Taylor, 1989; Rehfuess, 1989; Skelly, 1989). Acidic deposition has both direct and indirect effects on plants and associated microorganisms (Campbell et al., 1988; Heagle, 1973; Killiam et al., 1983, Magan and McLeod, 1991; Musselman and McCool, 1989; Skelly, 1989). The sum of these effects can result in an increase or a decrease in disease severity. Acidic deposition inhibits many fungi, especially rusts and wood-decay organisms (Heagle, 1973; Magan and McLeod, 1991; Shafer et al., 1985; Shriner, 1978; Smith, 1990). Bruck and Shafer (1983) proposed the explanation that acidic deposition wounds host tissues, and induces generalized resistance responses effective against obligate parasites, which prefer a vigorous host. However, because wounding and stress increase the rate of

635

senescence, acidic deposition could increase susceptibility to facultative parasites, which prefer a weakened host (Bruck and Shafer, 1983). In some plants, acidic rain increases leaf wettability, foliar water-holding capacity, foliar nutrient uptake, and the leaching of polar solutes (Evans, 1982; Lepp and Fairfax, 1976; Norby et al., 1986; Percy and Baker, 1988). Also, acidic fog affects water relations (Eamus et al., 1989; Mengel et al., 1989) in some plants. Such effects as these may have more impact on trees than on annual plants. Through the soil acidic rain can also indirectly produce cumulative effects. It can increase the concentration of aluminum and base cations in the soil solution and provide nitrogen (N), which is a limiting nutrient in many southeastern soils (Binkley et al., 1989).

Madden and Campbell (1987) noted that the effects of air pollutants on pathogen virulence and host resistance have rarely been studied. Most of the literature considers effects on spore germination and penetration or the ultimate effects on disease severity. The mechanisms by which acidic rain influences disease severity are largely unknown.

The potential for complexity when a disease and a pollutant interact is illustrated by the effects of acidic deposition on Scleroderris canker caused by *Gremmeniella abietina* on Norway spruce (*Picea abies* L. Karsten). *G. abietina* infection is usually latent in Norway spruce. But acidic precipitation enables the pathogen to produce disease symptoms by reducing competition and enhancing spore germination (Barkland et al., 1984). Competition is reduced when acidic precipitation affects epiphytes and endophytes (Barkland and Unestam, 1988). At the same time, acidic precipitation causes ion leakage that enhances spore germination of *G. abietina*. Intriguingly, Scleroderris canker severity on Scots (Barkland and Unestam, 1988) and red pines (Bragg and Manion, 1984), which are normally more susceptible than spruce, is not affected by acidic precipitation treatments.

In 1993, Anderson et al. (1993) reported that simulated acidic rain (SAR) increased the susceptibility of dogwoods to anthracnose under laboratory conditions. Britton et al. (1996) demonstrated that pretreatment with SAR also increased susceptibility to natural inoculation in the field. However, the mechanism for this effect is unknown.

Acid conditions do not directly favor the pathogen. In fact, *D. destructiva* is inhibited by highly acidic conditions in vitro. Conidial germination on agar was zero at pH 2.0, but not significantly affected from pH 3.0 to 5.6 (Britton, 1989). Mycelial growth was also reduced by acidic conditions (Britton, 1993).

Several studies have examined the effects of acidic precipitation on dogwood foliage. Haines et al. (1980) reported no visible damage on dogwoods treated with pH 2.0 SAR. However, scanning electron microscopy studies have since shown that SAR treatments eroded epicuticular wax and altered trichome morphology of dogwood leaves (Brown et al., 1994; Thornham et al., 1992). Furthermore, Willey and Hackney (1991) demonstrated that there was increased leaching of calcium and magnesium ions from dogwood leaves treated with SAR droplets. Plant leachates also often contain sugars and amino acids, although these have not been investigated in dogwood. Leakage of such foliar nutrients may either stimulate or

inhibit pathogenic fungi (Blakeman, 1973). An excessive loss of nutrients through leaching could also stress the host. Stress from other sources, for example, drought, increases susceptibility to anthracnose (Gould and Peterson, 1994).

In 1992 and 1993, we established experiments to determine whether the observed increase in dogwood susceptibility to anthracnose was the result of aboveground factors (e.g., cuticular erosion) or belowground factors (e.g., altered nutrient availability). We designed other experiments to determine whether plants exposed to SAR were more stressed or more susceptible to drought than plants not exposed to SAR. The results reported here offer intriguing clues to the complex nature of this host–parasite interaction.

Materials and Methods

Soil vs Foliar Effects

To separate soil and foliar effects, we applied pH 2.5 and pH 5.5 SAR to the soil, to the foliage, or both. The experiment as described in the following sections was run twice in 1992 and twice in 1993. The experiments for each year were conducted simultaneously in order to complete ten pretreatment applications and expose the seedlings to natural inoculation early in June. We started in January with one-year-old flowering dogwood seedlings from the Georgia Forestry Commission nursery near Montezuma. In February, we planted them in 5-l containers in a mixture of equal parts by volume of peat moss, perlite, and topsoil, and placed them in an air-conditioned greenhouse maintained at 23 to 27 °C in Dry Branch, Georgia. We fertilized all the seedlings once two weeks after planting, with an excess volume of a dilute commercial fertilizer (15:30:15 at 100 ppm N).

After leaf emergence, we selected 240 seedlings for uniformity in size and vigor. We prepared SAR solutions, adjusted to pH 2.5 or pH 5.5 with a 0.65 molar (M) mixture of sulfuric and nitric acids in approximately the same ratio found in ambient rain (70 mequiv SO_4^{-2}:30 mequiv. NO_3^-) (Shafer et al., 1985).

We assigned sixty seedlings to each of the following four pretreatments: 1) soil/acid, which received pH 2.5 SAR on the growing medium surface and pH 5.5 SAR on the foliage, 2) foliage/acid, which received pH 2.5 SAR on the foliage and pH 5.5 SAR on the growing medium surface, 3) both/acid, with pH 2.5 SAR applied to both the growing-medium surface and foliage, and 4) none/acid, with pH 5.5 SAR applied to both the growing-medium surface and foliage. Before each rain event, we tied a plastic bag around the root collar of each seedling, covering the growing medium and pot. We applied the foliar pretreatments using a rain simulator (Chevone et al., 1984), and we removed the plastic bags between rain events. We applied treatments to the growing medium by pouring 300 ml of SAR of the appropriate pH directly on the soil surface. Additionally, we applied SAR of the appropriate pH as needed to maintain adequate levels of soil moisture for a total of about 5-l per container over the 10-week duration of the pretreatments.

After SAR pretreatment, we transported most of the dogwood seedlings to

Coweeta Hydrologic Laboratory in southwestern North Carolina and placed them under mature dogwoods that were naturally infected with *D. destructiva*. These seedlings received natural rainfall thereafter. A subgroup of forty-eight seedlings were kept at Dry Branch, Georgia for physiological studies.

In late June and September, we visually estimated the percent leaf area infected for each seedling. We used the means for the eight seedlings remaining in each pretreatment in each replication as data points (n = 6) in a regression analysis. An analysis of variance (ANOVA) was also performed, and the means were separated using Duncan's Multiple Range Test. Significant interaction between soil and foliar applications in 1993 necessitated comparison of simple effect means by Duncan's Multiple Range Test.

Plant Vigor and Drought Tolerance

At the end of the rain pretreatment period, we removed two seedlings from each pretreatment in each replication (forty-eight seedlings) and kept them in the greenhouse in Georgia for further study. We saturated the growing medium with deionized water, allowed it to drain, weighed it, and measured predawn xylem pressure potential (PXPP), midday net photosynthesis (P_{net}), and stomatal conductance (g_1). We used a pressure bomb (Soil Moisture Equipment Corp.) to measure PXPP, and a LI-6200 portable photosynthesis system (Li-Cor, Inc.) to measure P_{net} and g_1. Half the seedlings from each rain treatment continued to receive adequate amounts of deionized water; the other half received no additional water for the duration of this study. We repeated all measurements at approximately weekly intervals. We harvested the water-stressed seedlings when they stopped showing a positive rate of P_{net} and recorded fresh weights for leaves, stems, roots, and soil dry weight. We measured leaf areas with a Li-Cor leaf area meter (Li-Cor, Inc.) and we also recorded oven dry weights. We then mailed leaf samples and soil samples to the UGA Soil Testing Laboratory, Cooperative Extension Service in Athens, Georgia for nutrient analyses.

Results

Soil vs Foliar Effects

Application of pH 2.5 SAR directly on the growing medium increased disease severity in three of four experiments (Table 34.1). Applications of pH 2.5 SAR to the foliage alone did not increase disease in either year. However, in the second experiment in 1993, applications to both the foliage and the growing medium significantly increased disease over applications to the growing medium alone (Table 34.1).

Some abscission of uninfected leaves was noted in August of 1993. Earlier than

Table 34.1. Percentage of Leaf Area Infected with Dogwood Anthracnose Following Pretreatments with Either pH 2.5 or 5.5 Simulated Acidic Rain on the Soil and Foliage

Pretreatment with pH 2.5 SAR[1]	1992		1993	
	Experiment 1	Experiment 2	Experiment 1	Experiment 2
Soil only	5.7[2]	2.0[3]	1.0[2]	4.1[4]b
Soil and foliage	5.8	3.1	0.5	7.4 a
Foliage only	3.5	2.5	0.1	0.9 c
None	2.9	2.2	0.1	0.9 c

[1] Foliage or soil not treated with pH 2.5 simulated acidic rain (SAR) was treated with pH 5.5 SAR.
[2] Soil application treatments exhibited significant increase in disease (ANOVA main effect at $P < 0.01$). Foliage application main effect and soil × foliage application interactions were not significant.
[3] No significant differences in this experiment.
[4] Significant soil × foliage application interactions occurred. Simple effects tested by ANOVA. Means followed by the same letter do not differ significantly at $P \leq 0.05$ according to Duncan's Multiple Range Test.

expected for autumn leaf fall, this abscission was more common in Experiment 2, which was exposed to natural inoculum in a location receiving less light than experiment 1. The amount of leaf loss was small (2 vs 4%), but significantly less ($P = 0.05$) in seedlings receiving pH 2.5 SAR on the growing medium than in those receiving normal rain (pH 5.5).

Plant Vigor and Drought Tolerance

Well-watered seedlings that received pH 2.5 rain on the growing medium showed significantly higher rates of P_{net} and g_1 on most test dates than trees that received pH 5.5 rain on the medium, regardless of the pH of the foliar rain pretreatment. In water-stressed seedlings, those that received pH 2.5 rain on the growing medium initially showed higher rates of P_{net} and g_1 than those that received pH 5.5 rain on the medium. But after seventeen days, these rates reversed and water-stressed seedlings that received pH 2.5 rain on the medium showed lower rates of P_{net} and g_1 than those receiving pH 5.5 rain (Figures 34.1 and 34.2).

A steady decline of PXPP was observed in all water-stressed seedlings (Figure 34.3). Early in the study, the difference in PXPP between rain treatments was not significant, but after seventeen days without water, water-stressed trees that received pH 2.5 SAR on the growing medium showed significantly lower PXPP than seedlings that received pH 5.5 SAR on the medium (Figure 34.3). At the end of the study, leaf area and dry weight were significantly greater in plants that received pH 2.5 SAR only on the medium than in plants that received pH 2.5 SAR only on the leaves (Table 34.2). Stem weight followed the same trend, but the difference was not significant. The differences in root weights and shoot/root ratios were not significant.
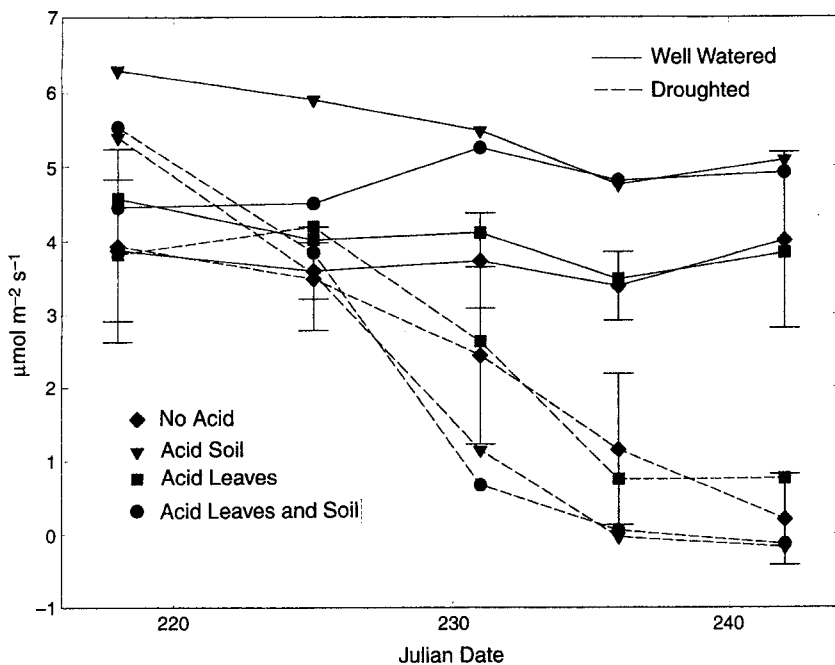
Figure 34.1. Net photosynthesis (P_{net}) of dogwood seedlings that were pretreated with either pH 2.5 or 5.5 simulated rain on foliage, soil, or both, on five measurement dates after two drought stress treatments were applied.
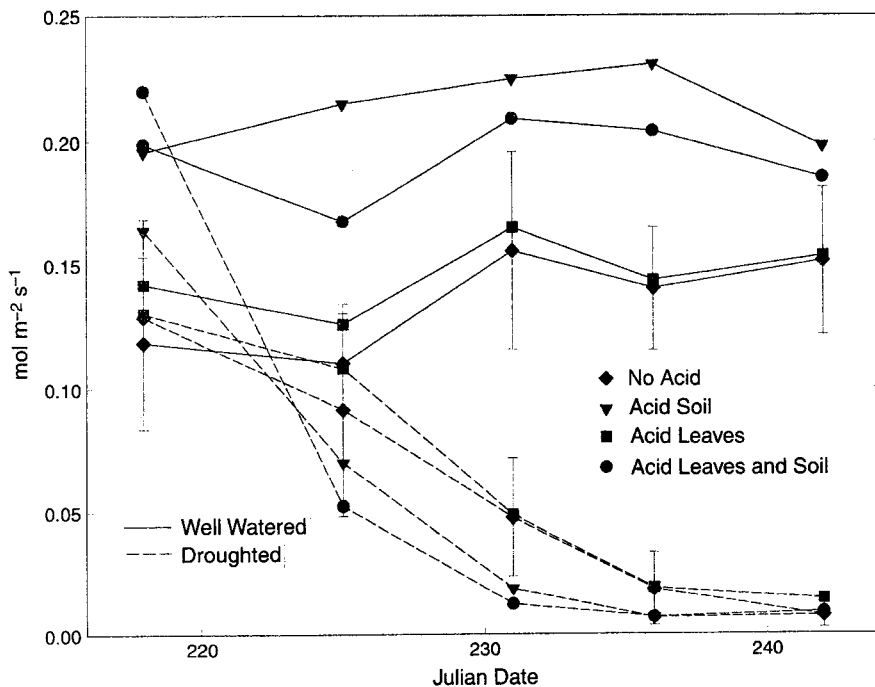
Figure 34.2. Stomatal conductance (g_1) of dogwood seedlings that were pretreated with either pH 2.5 or 5.5 simulated rain on foliage, soil, or both, on five mesurement dates after two drought stress treatments were applied.
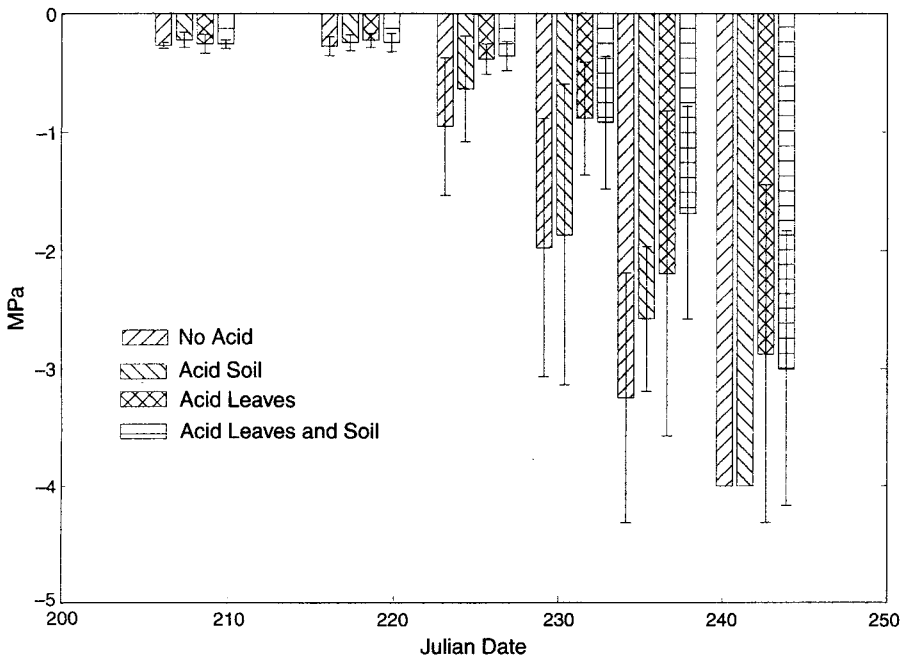
Figure 34.3. Predawn xylem pressure potential (PXPP) of dogwood seedlings that were pretreated with either pH 2.5 or 5.5 simulated rain on foliage, soil, or both, on five measurement dates after two drought stress treatments were applied.

Summary

Although other research has shown that acidic rain treatment erodes dogwood foliage (Brown et al., 1994; Thornham et al., 1992) and enhances nutrient leakage (Willey and Hackney, 1991), the studies reported here clearly demonstrate that the more important mechanisms for increased anthracnose severity are soil-mediated.

Acidic rain has the potential to affect a number of soil or root processes, but N fertilization appears to be the most probable explanation for the increased growth observed. All seedlings were lightly fertilized once during the study, but the SAR treatments applied to the medium provided more than twice this amount of N when the pH was 2.5 but they received almost no additional N when the pH was 5.5. Seedlings growing in the medium treated with pH 2.5 rain had significantly higher leaf N than seedlings growing in the pH 5.5 rain-treated medium (Table 34.2). Ludovici (1990) found SAR N increased growth in *Pinus taeda* L. (Hudler, 1985). Nitrogen fertilization would also explain the reduced leaf abscission observed in 1993, following soil applications of pH 2.5 rain. The tendency of high levels of soil N to delay leaf abscission has been recognized for many years (Kozlowski, 1971). Further studies are underway to determine whether N fertilization alone increases susceptibility to anthracnose. Neely (1986) found the

Table 34.2. Effects of Soil and Foliage Pretreatments with pH 2.5 or 5.5 Simulated Acid Rain on Date of Death, Biomass, Leaf Area, and Leaf Nitrogen Content and Shoot/Root Ratio of Drought-Stressed Trees

Pretreatment with pH 2.5 SAR[1]	Mean Julian date of death	Leaf biomass (gm)	Stem biomass (gm)	Root biomass (gm)	Leaf area (cm^2)	Leaf N content %	Shoot/Root Ratio
None	247 a[2]	5.7 ab	9.55 ab	22.2 a	780 b	0.75 b	0.67 a
Foliage only	244 ab	4.9 b	8.58 b	19.6 a	787 b	0.72 b	0.70 a
Soil only	237 bc	6.7 a	10.39 ab	22.2 a	1110 a	0.90 a	0.76 a
Soil & foliage	234 c	6.4 ab	11.13 a	23.2 a	1073 a	0.89 a	0.76 a

[1] Foliage or soil not treated with pH 2.5 SAR was treated with pH 5.5 SAR.
[2] Numbers within columns followed by the same letter are not significantly different (P ≤ 0.05) according to Duncan's Multiple Range Test.

reverse in *Gnomonia leptostyla* infection of black walnut; in that host–pathogen system, the number of anthracnose lesions decreased with increasing leaf N content.

Because acidic deposition can affect the ability of plants to regulate internal moisture (Eamus et al., 1989; Mengel et al., 1989), increased susceptibility to drought could be another explanation for the effect of acidic rain on the intensity of dogwood anthracnose. Among water-stressed seedlings, those growing in media treated with pH 2.5 rain died ten days earlier than seedlings growing in media treated with pH 5.5 rain. Because these seedlings were larger, increased water usage may explain the faster mortality rate. The increase in leaf area associated with soil applications of pH 2.5 rain could also make the seedlings more susceptible to drought stress if leaf growth occurred at the expense of root growth. Although the trend in shoot/root ratio supports this hypothesis, differences were not significant with this small sample size. Norby et al. (1986) reported a similar increase in moisture stress resulting from acidic rain treatments that was associated with increases in growth rates of red spruce.

Factors that reduce dogwood vigor are believed to increase anthracnose severity (Gould and Peterson, 1994). This study suggests, however, that exposure of the soil to acidic rain actually increases vigor if the seedlings are well watered. Ludovici (1990) also found that soil applications of SAR increased root and shoot weight of *Pinus taeda* L. seedlings. An increase in photosynthesis following SAR treatments was also reported for *Phaseolus vulgaris,* but it was accompanied by a decrease in carbohydrate production and growth rate (Ferenbaugh, 1976). Ferenbaugh (1976) suggested that uncoupling of photophosphorylation explained this apparent anomaly. This possible explanation does not apply to dogwood because soil applications increased growth and photosynthesis in this study. Smith (1990) described a potential interaction of an intermediate dosage of air pollutant with temperate forest ecosystems. In this model interaction, individuals of a given species would be expected to undergo nutrient stress, decreased photosynthesis rate, decreased reproductive rate, and reduced vigor, thus becoming increasingly predisposed to disease and insect pests. The data presented here suggest that although well-watered plants can be more vigorous after receiving acidic rain treatments, water-stressed trees died faster following acid rain treatments. In nature, midsummer drought stress is common in dogwood, which is shallow-rooted. Therefore, it is important to remember that the host response to acidic precipitation interacts significantly with other climatic and site factors.

Most research on the interactions between acidic rain and dogwood anthracnose has focused on foliar mechanisms (Brown et al., 1994; Thornham et al., 1992). The results of these studies indicate that the belowground effects of acidic rain are more important. Acidic rain can change the availability of N and other nutrients (Binkley et al., 1989) and it may be that changes in nutrient composition or changes in carbohydrate levels make the leaves a better substrate for growth of the fungus. Perhaps an increase in succulence brought on by the addition of N in the SAR solution to the growing medium makes it easier for fungal hyphae to penetrate the leaf tissue. Unfortunately, too little is known about the effects of

acidic rain on dogwood anthracnose to determine how important it is outside an experimental situation, or how to counteract its effects.

It seems improbable that acidic rain alone is responsible for the decimation of dogwood experienced in the Northeast and in the southern Appalachian *Cornus florida* L. population. Our studies do indicate, however, that acidic rain may play a role by increasing host vulnerability to drought stress, as well as increasing inherent susceptibility of dogwood to anthracnose.

The impact of anthracnose on dogwood populations varies by location (Langdon et al., 1993). At Catoctin Mountain National Park, dogwood populations have declined 94% in just ten years. Most surviving trees are growing in locations with partial exposure to direct sunlight. Understory trees, which receive only 2% of ambient photosynthetically active radiation (Chellemi and Britton, 1992) probably have few carbohydrate reserves to expend on refoliation after fungal attack. The microclimate of understory trees is also more favorable to infection than that of partially exposed trees (Chellemi and Britton, 1992). Temporary conditions favorable to severe infection, which might include acidic precipitation, may have profound direct and indirect effects on the forest understory in just a few years.

The long-term effects of species replacement in the understory could be numerous and significant. Dogwood fruit are high in fat, an important energy source for winter survival of migratory birds and other animals. The fruit makes up 25 to 50% of the diet of the evening grosbeak, and 5 to 10% of the diet of ruffed grouse, wild turkey, cardinals, robins, gray-checked and wood thrushes, and cedar waxwings (Halls, 1977; Martin et al., 1951). Dogwood leaves and twigs are high in calcium (DeGraff and Whitman, 1979), and are used by bear, beaver, rabbit, racoon, fox squirrel, chipmunks, deer, and moose. The decline of this essential nutrient may have long-term dietary consequences.

Dogwood also plays an important role in calcium cycling in forest soils. The foliage accumulates calcium, and leaf litter contains 2.0 to 3.5% calcium (dry weight) (Vimmerstedt, 1957). Thus, species replacement of the dogwood could have sweeping consequences for other vegetation.

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